# Dynamic Energy Budget (DEB) Models of Bivalve Molluscs Inhabiting British Columbia Coastal Waters: Review of Existing Data and Further Directions for Data Collection

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# DYNAMIC ENERGY BUDGET (DEB) MODELS OF BIVALVE MOLLUSCS INHABITING BRITISH COLUMBIA COASTAL WATERS: REVIEW OF EXISTING DATA AND FURTHER DIRECTIONS FOR DATA COLLECTION

by

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## ABSTRACT

Filgueira, R., Guyondet, T., Comeau, L.A., and Sutherland, T.F. 2016. Dynamic Energy Budget (DEB) models of bivalve molluscs inhabiting British Columbia coastal waters: Review of existing data and further directions in data collection. Can. Tech. Rep. Fish. Aquat. Sci. 3173: vii + 28 p.

The use of ecosystem models in aquaculture sites is becoming a common methodology for research and management. Two components are key for a successful model, the conceptual design and the data available for calibration and validation. Regarding conceptual design in the specific field of bivalve energetics, Dynamic Energy Budget (DEB) theory is among one of the most accepted approaches with DEB models available for several species. However, specific model calibration to local conditions is usually required and DEB parameters for many bivalve species are yet to be estimated. The parameterization of a DEB model requires an extensive range of shellfish and supporting ecosystem datasets, some of which may be currently available in the literature. In this study, a review of existing DEB models developed for bivalve molluscs inhabiting British Columbia coastal waters was carried out. In addition, potential datasets for the parameterization of new DEB models were reviewed with a focus on six prevalent bivalve molluscs inhabiting southern British Columbia. Cost-effective experiments designed to cover data gaps are also recommended for future studies. The review is completed with a description of the main DEB parameters and mathematical tools that can be used to parameterize the model for each species, as well as an example using Manila clams as a case-study.

## RÉSUMÉ

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L'emploi de modèles écosystémiques pour des sites aquacoles est de plus en plus répandu, aussi bien dans un cadre de recherche scientifique que pour la gestion de ces activités. Le succès du développement de tels modèles repose sur deux composantes principales : la représentation conceptuelle du système et la disponibilité des données pour la calibration et la validation du modèle. Dans le contexte de la bioénergétique des bivalves, la théorie DEB (Dynamic Energy Budget) propose une des représentations conceptuelles les plus reconnues et ce type de modèle est déjà disponible pour plusieurs espèces. Toutefois, une calibration du modèle en fonction des conditions environnementales locales est généralement requise et les paramètres DEB restent encore à être estimés pour de nombreuses espèces de bivalves. L'estimation des paramètres d'un modèle DEB nécessite des jeux de données diversifiés sur les bivalves et leur environnement, certains d'entre eux pouvant être extraits de la littérature existante. La présente étude établie une revue des modèles DEB existants et des jeux de données d'intérêt pour la paramétrisation de nouveaux modèles pour les six principales espèces de mollusques bivalves des eaux côtières du sud de la Colombie Britannique. Une série d'expériences ciblées est également recommandée pour combler les lacunes des jeux de données existants par de futures études. Cette revue comprend enfin, une description des principaux paramètres DEB et des outils mathématiques disponibles pour déterminer leur valeur pour différentes espèces. L'utilisation de ces outils est illustrée par une étude de cas portant sur une espèce de palourde.

## 1.0. INTRODUCTION

Ecosystem models are becoming integral in aquaculture management (e.g. Byron et al. 2011, Ferreira et al. 2013, Guyondet et al. 2015). The possibility of generating *a priori* information on alternative management scenarios (e.g. Filgueira et al. 2014a) and the potential effects of unanticipated stressors (Nobre et al. 2010) are highly valuable to establishing long-term management plans. In the particular case of bivalve aquaculture sites, although models can vary in ecological complexity and spatial resolution (see review in Filgueira et al. 2015), in general they can provide some insight into bivalve growth and ecosystem effects. A common strategy in ecosystem modelling is to develop independent submodels for the different species of interest (e.g. *Mytilus edulis*, *Crassostrea virginica*) or functional groups (e.g. phytoplankton, zooplankton) that are coupled together to simulate ecosystem-scale processes. In the case of bivalve molluscs there are two main modelling approaches to simulate bivalve physiology and growth: Dynamic Energy Budget (DEB, Kooijman 2010) and Scope For Growth (SFG, Winberg 1960). Although both approaches have been successfully applied to model bivalve growth and bioenergetics (Filgueira et al. 2011, Larsen et al. 2014) there are fundamental differences between them. DEB is a mechanistic theory based on the assumption that assimilated energy is first stored in "reserves" which in turn are utilized to fuel other metabolic processes (Kooijman, 2010). DEB also provides an unifying theory at the individual level through the entire life-cycle and at the inter-specific level through the use of common parameters. On the contrary, SFG is based on an empirical energy balance, assuming assimilated energy to be immediately available for catabolism, and using allometric relationships to extrapolate to differently-sized organisms. Accordingly, DEB models can be theoretically applied to the full range of environmental conditions but SFG models require specific calibration for each location. This advantage of DEB theory has become critical in recent years and is reflected in an international scientific effort towards DEB modelling, especially in marine sciences (van der Meer et al. 2014). A detailed analysis of strengths and weaknesses of the SFG and DEB approaches in the context of bivalve modelling has been provided by Filgueira et al. (2011) and Larsen et al. (2014).

The success of a model in providing reliable results depends on (1) the conceptual design of a model, and (2) the data available for parameter calibration and model validation. The core equations of DEB describe the individual in terms of three state variables: reserve(s), structure, and maturity/reproduction (Figure 1). The energy assimilated from food is stored as reserves; a fixed fraction of this energy ($\kappa$) is directed towards maintenance and growth of the structural body, and the remainder ($1-\kappa$) is directed towards maturity maintenance and maturation or gamete production depending on the life cycle stage of the organism. Although this conceptual design is common to all existing DEB models, each model usually includes particular equations to adapt the core code to a given species. This is especially relevant in the case of bivalves, for which a range of approaches have been developed to mathematically define their feeding behavior (Alunno-Bruscia et al. 2011) by using different food proxies (Bourlès et al. 2009, Picoche et al. 2014), including different food sources in the ingestion law (Alunno-Bruscia et al. 2011) or applying of the concept of "synthesizing units" (Saraiva et al. 2011a). Regarding available data, it is important to

highlight that modelling best practices require independent datasets for parameter calibration and model validation. Parameter calibration in DEB modelling has been achieved following two methods: independent estimation of each parameter (van der Meer 2006, van der Veer et al. 2006) or simultaneous calibration of all parameters using mathematical algorithms (Lika et al. 2011). The first one relies on specific datasets for a direct estimation of each parameter, which can be challenging due to the high level of abstraction of some parameters and the fact that their dimensions are often related to the state variables, reserve(s), structure and maturity/reproduction, which cannot be directly observed (Lika et al. 2011). Ultimately, this implies the formulation of multiple assumptions to directly estimate DEB parameters (e.g. van der Veer et al. 2006). In order to circumvent these shortcomings, mathematical procedures can be used to find the optimal set of parameters that minimizes the discrepancies between the results of the model and datasets chosen by the user. Given that the set of optimal parameters is mathematically estimated and not directly derived, these approaches rely on the use of multiple datasets to minimize the risk of getting a good fit for the wrong reasons. This mathematical approach estimates all the parameters using all available datasets for a given species in a single-step-procedure, which brings more coherence to the set of parameters. An example of this approach can be found in Saraiva et al. (2011b). Intermediate approaches in which some parameters are directly measured and some are mathematically estimated are also common in the literature (e.g. Rosland et al. 2009, Filgueira et al. 2011, Larsen et al. 2014). As stated above, once the parameters of the DEB model are calibrated, an independent dataset is required for validation.

Our review is part of a larger project that aims to explore the bivalve carrying capacity of Baynes Sound, British Columbia. To achieve that goal a fully spatial hydrodynamic-biogeochemical model will be constructed in FVCOM. Our review is focused on modelling the bioenergetics of the most common bivalve species inhabiting Baynes Sound, that is, the blue mussel *Mytilus edulis*, the Pacific oyster *Crassostrea gigas*, the Manila clam *Venerupis philippinarum*, the littleneck clam *Protothaca staminea*, the varnish clam *Nuttallia obscurata* and the butter clam *Saxidomus gigantea*. Accordingly, the following goals are pursued:

- Describe a generic standard DEB model for bivalves and identify mathematical tools that can be used to parameterize the model for each species.
- Review existing sets of DEB parameters for these species.
- Review existing datasets that could be used to calibrate new models for these species (an example for Manila clam is presented).
- Identify data gaps and suggest future cost-effective strategies to optimize data collection in the context of DEB modelling.

## 2.0. DEB AND MODELLING TOOLS

### 2.1. DEB model and core parameters

The general bivalve DEB model (Figure 1, Table 1) is based on Pouvreau et al. (2006), which has been commonly used in the literature (e.g. Rosland et al. 2009, Guyondet et al. 2010, Filgueira et al. 2014b). The description of the model follows the

original notation by Kooijman (2010), in which [] denote quantities expressed as per unit structural volume, {} denote quantities expressed as per unit surface area of the structural volume and a dot over a symbol denotes a rate, or a dimension per time. Although DEB allows for simulation of the complete life cycle (embryo, larva, juvenile and adult), in this case it has been initialized at the juvenile stage due to the uncertainty/lack of data available to parameterize the embryo and larval stages. A brief description of the model is presented in Table 1 and a more thorough presentation of the model and the equations are given in Pouvreau et al. (2006) and Rosland et al. (2009). The following section describes the core parameters of DEB and the datasets that would be required according to van der Veer et al. (2006) to independently estimate their values.

The **shape coefficient**, $\delta_M$, determines how a specific length measurement relates to structural body mass. The shape coefficient can be estimated by analyzing length vs body mass allometries and assuming isometric growth. Seasonal allometries will permit dismissal of any effects caused by the reproduction cycle, improving the estimation of $\delta_M$.

The **maximum surface-area-specific ingestion rate**, $\{\dot{p}_{Xm}\}$, informs about the maximal ingestion rate of an individual of a given size. In bivalves, ingestion rate is the balance between clearance rate, the volume of water cleared of particles per unit of time, and pseudofaeces production rate, the amount of particles per unit of time that are cleared but rejected prior to ingestion. It has been suggested that ingestion rate is at a maximum when the production of pseudofaeces begins (Winter 1978). Hence the estimation of $\{\dot{p}_{Xm}\}$ can be calculated as the product of clearance rate and the food concentration corresponding to the initiation of a pseudofaeces production phase. The combination of this parameter with measured absorption efficiency ($AE$) provides the maximum surface-area-specific absorption rate, $\{\dot{p}_{Am}\}$.

The **volume-specific maintenance costs**, $[\dot{p}_M]$, cannot be estimated directly and precisely from experimental data. A common indirect approach for $\dot{p}_M$ estimation is to assume that respiration mainly reflects maintenance metabolism of a starved filter-feeder. Therefore, the parameter can be estimated by measuring respiration rate in starvation experiments (from weeks to months depending on the species). However, the starvation experiment should not be too long, otherwise structural mass could be broken down as energy, altering the estimation of $[\dot{p}_M]$.

The **volume-specific costs for growth**, $[E_G]$, cannot be directly estimated either. One approach is to use the energy content of the structural body mass of an individual after starvation, just prior to mortality. It is assumed that the minimum in somatic mass reflects an individual consisting only of structural mass with hardly any remaining reserves (van der Veer et al. 2006). Combining length and structural body mass of starved individuals with conversion factors that reflect the costs for material synthesis $[E_G]$ can be derived.

The **maximum storage density**, $[E_m]$, represents the capacity of an individual to store energy in reserves. $[E_m]$ can be indirectly estimated by measuring the difference in average somatic mass index of the studied organism at the end of winter, when stores are low, and at the end of the growing season, when stores are high. The difference is

considered to represent a minimum estimate of $[E_m]$.

The **fraction of utilized reserves to growth and maintenance**, κ, can be derived from the theoretical relationship among maximum volumetric length, κ, $\{\dot{p}_{Am}\}$ and $[\dot{p}_M]$ (van der Veer et al. 2006):

$$V_m^{1/3} = \kappa \times \frac{\{\dot{p}_{Am}\}}{[\dot{p}_M]}$$

where $V_m^{1/3}$, volumetric length, can be calculated by multiplying the shape coefficient by the observed maximum length.

The **half-saturation constant**, $X_K$, is the food level at which ingestion rate reaches half the maximum rate. This parameter is part of the ingestion function, f, which scales the ingestion rate to the food concentration following a Holling II functional response. Although it can be theoretically derived (see eq. 9 in Rosland et al. 2009), $X_K$ is usually calibrated using mathematical algorithms (e.g. Rosland et al. 2009, Filgueira et al. 2011, Larsen et al. 2014).

Given the effect of temperature on the physiological response of the organisms, all of the physiological rates in DEB are corrected according to the extended Arrhenius law (Kooijman, 2010):

$$\dot{k}(T) = \dot{k}_1 \times \exp\left(\frac{T_A}{T_1} - \frac{T_A}{T}\right) \times s(T)/s(T_1)$$

$$s(T) = \left(1 + \exp\left(\frac{T_{AL}}{T} - \frac{T_{AL}}{T_L}\right) + \exp\left(\frac{T_{AH}}{T_H} - \frac{T_{AH}}{T}\right)\right)^{-1}$$

where $T$ is the absolute temperature (K), $T_1$ is the reference temperature (K), $\dot{k}(T)$ is the physiological rate at temperature $T$, $\dot{k}_1$ is the physiological rate at temperature $T_1$, $T_A$ is the Arrhenius temperature, $T_L$ and $T_H$ the lower and upper tolerance range, respectively, and $T_{AL}$ and $T_{AH}$ the rate of physiological rate decrease at lower and upper boundary, respectively. The **Arrhenius temperature**, $T_A$, and all related parameters $T_L$, $T_H$, $T_{AL}$ and $T_{AH}$ can be estimated using any physiological rate at different temperatures.

### 2.2. Mathematical tools for model calibration

The use of mathematical tools for model calibration is a well-known approach to estimate parameters when they cannot be directly measured. There are two main techniques to achieve this goal: (1) randomized sets of parameters, and (2) optimization algorithms. The first approach is based on the generation of randomized sets of parameters within a range of pre-defined values followed by the analysis of the model performance for that set of parameters (e.g. Duarte et al. 2010, Sonier et al. *in press*). The set of parameters that produces the best fit between predicted and observed values is identified and selected as the best solution. This approach requires testing a high number of combinations of parameters in order to ensure that valid combinations are not randomly discarded without testing. The second approach is based on the use of optimization algorithms that are specifically designed to find the

set of parameters that minimizes the discrepancies between predicted and observed values. Different methods that include optimization procedures have been used in the literature in the context of DEB modelling, including non-linear Nelder-Mead (Rosland et al. 2009); PEST, which is based on the Gauss-Marquardt-Levenberg algorithm (Filgueira et al. 2014b); and the covariation method, which is based on the maximum likelihood function (Lika et al. 2011). The covariation method is included in the "add_my_pet" collection (http://www.bio.vu.nl/thb/deb/deblab/add_my_pet/), which provides the code (in Matlab and Octave) to estimate DEB parameters. The "add_my_pet" portal also compiles the DEB parameters estimated with that code for more than 375 species.

The advantage of using optimization algorithms is obvious given that they aim to identify the optimal parameter set, which could be discarded when using the randomized approach. However, most optimization algorithms are not straightforward tools, particularly when several parameters are simultaneously optimized. Under these conditions the probability of stopping the optimization process at a local minimum increases. A local minimum in the context of optimization is a "good" solution to the problem in a certain region of the optimization space. Despite being a good solution, a local minimum is not the global optimum, the optimal solution among all possible solutions. On the contrary, the use of random set of parameters is not affected by the presence of local minimums. The use of random set of parameters has been tested in the example of Manila clam presented in this study. In total, 100,000 different sets of parameters were randomly selected from a predefined range based on a literature review of existing Manila clam models and related species. The best solution was defined as the smallest deviation ($D$) between simulated and observed values simultaneously for all datasets, which was calculated following:

$$D = \frac{1}{N}\sum_{n=1}^{N}\left(\frac{1}{J}\sum_{j=1}^{J}\frac{|M_s(j) - M_o(j)|}{M_o(j)}\right)$$

where $n$ is the dataset index, $N$ the total number of datasets, $j$ the observation index for a given dataset, $J$ the total number of observations for a given dataset, and $M_s$ and $M_o$ are simulated and observed values, respectively. In this example $M_s$ and $M_o$ includes values of shell length and dry weight.

The data used for calibration according to these mathematical techniques can range from growth curves to allometric relationships and forcing data, i.e. food density and temperature, for each dataset. The more datasets available, the more robust is the calibration.

### 2.3. Model validation and sensitivity analysis

Validation is a critical aspect of modelling best practices. Independent datasets must be used to guarantee that model parameterization is not only valid for the datasets that were used during the calibration process. In the context of bivalve modelling, the following datasets are the minimum needed for validation:

- Growth in terms of dry weight and length over a long period of time,
- Forcing datasets, i.e. food density and temperature.

Given the review nature of this study, model validation has not been performed for the Manila clam example.

Sensitivity analysis is the study of how the uncertainty in the model outcomes can be explained by uncertainty of the model parameters (Saltelli 2002). A simple sensitivity analysis is to modify a parameter by a certain amount that represents the uncertainty in the parameter estimation, usually ±10%, run the model and quantify the change in the model performance. A sensitivity analysis has been carried out for the existing DEB models by increasing and decreasing 14 parameters by 10 % (12 parameters described above in Section 2.1. as well as *AE* and the ratio dry weight:wet weight for tissue, DW:WW) under the typical environmental conditions of Baynes Sound (see below). The impact of the change of each parameter on shell length (SL), dry weight (DW), dry weight minus gonads (DWmG), clearance rate (CR), respiration rate (RR) and excretion rate (ER) was analysed at the end of each simulation by comparing to the base scenario (average literature parameters) and expressed as:

$$Impact\ (\%) = \frac{M_{average} - M_{sensitivity}}{M_{average}} \times 100$$

where *M* is the SL, DW, DWmG, CR, RR or ER value during the last day of simulation and *average* and *sensitivity* stand for the *M* value obtained with the average set of parameters and the modified parameter considered in the sensitivity test, respectively. The maximum impact of one parameter on the response variable at the end of the simulation was calculated following:

Maximum impact = Maximum [Absolute (Impact +10%), Absolute (Impact -10%)]

The DEB model during the sensitivity analysis has been forced with satellite sea-surface temperature (Figure 3). Chlorophyll-a. MODIS Level-3, global, daily, 4 km standard mapped images (2013 reprocessing) have been used for this task. The vertices of the area of interest for satellite subsetting are defined by 49.4269°N, 49.7002°N, -124.9978°E and -124.6792°E. Data from September 2002 till August 2015 have been analyzed to define the average annual trends plotted in Figures 2 and 3. Mean values were used to force the DEB model for 365 days (Jan 1$^{st}$ - Dec 31$^{st}$).

## 3.0. REVIEW OF EXISTING DATA

### 3.1. Mussel (*Mytilus edulis*)

*Mytilus edulis* is the most studied species in the context of DEB modelling. Among the available set of parameters, four studies should be reviewed (Table 2). Chronologically, van der Veer et al. (2006) provided the first set of DEB parameters that has been widely used. Following that set of parameters and the core DEB equations provided by Pouvreau et al. (2006) (see above), Rosland et al. (2009) used the DEB model to simulate mussel growth in Norwegian waters, introducing optimization tools to calibrate parameters with high uncertainty. Saraiva (2014) performed a full review of the mussel DEB model and Saraiva et al. (2011a)

highlighted that fact that the set of parameters provided by van der Veer et al. (2006) and Rosland et al. (2009) violate the principle of mass conservation. However, the new set of parameters reported by Saraiva et al. (2011a) are estimated using mostly wild populations of mussels, whose growth is below that observed for cultured mussels. In particular, the low maximum surface area-specific ingestion rate, $\{\dot{p}_{Xm}\}$, reported by Saraiva et al. (2011a) is remarkable, as it is too low to provide enough energy to explain the growth observed in cultured populations. In a further study, Maar et al. (2015), built up on Saraiva's parameters but obtained a $\{\dot{p}_{Xm}\}$ almost five times higher (Table 2), which would be enough to explain the higher growth of cultured mussels. An "add_my_pet" set of parameters is also available.

The sensitivity test for the average parameters (Table 3) reveals three clear conclusions. First, two parameters related to the food ingestion and energy absorption are identified as critical. Weights and physiological rates are very sensitive to maximum surface area-specific ingestion rate, $\{\dot{p}_{Xm}\}$, and absorption efficiency, AE. These two parameters together determine the maximum surface area-specific absorption rate, $\{\dot{p}_{Am}\}$, which in turn indicates the amount of energy that enters the reserve compartment and is available to fuel metabolic processes. The second important point to note is that the model is very sensitive to the function that corrects the individual physiological rates to the observed temperature. In particular, the model is very sensitive to the upper tolerance temperature, $T_H$, which is set at 23°C (~296K). Note that the change is more significant for physiological rates and weights rather than for shell length. This is due to the fact that shell length integrates the history of environmental conditions over time but weight and physiological rates are more dependent on current environmental conditions. For example, weight is affected by the reproductive cycle, e.g. spawning, which is highly dependent on temperature. In addition, shell length cannot shrink due to adverse environmental conditions whereas weight can be affected. Accordingly, shell length can be considered a more resilient body parameter than weight, which explains the lower sensitivity of shell compared to weights and physiological rates. Finally, the parameter $\kappa$, which splits the energy in the reserves towards structure or reproduction (Figure 1), is critical for the balance between structural tissue and gonads (DW and DWmG in Table 2), which in turn can be relevant for predicting the timing of spawning and reproductive potential of the population.

### 3.2. Oyster (*Crassostrea gigas*)

The work on *Crassostrea gigas* in terms of DEB modelling is also significant, starting with the work from Pouvreau et al. (2006). The authors of that paper have published several subsequent papers in which they have improved the parameters of the model. Consequently, in this review only the most recent paper from this group, Bernard et al. (2011), is presented (Table 4). Ren & Schiel (2008) indirectly estimated each parameter following van der Veer et al. (2006) and an "add_my_pet" set of parameters is also available (Table 4). The major differences among the three sets are related to maximum surface area-specific ingestion rate, $\{\dot{p}_{Xm}\}$, and the volume-specific maintenance costs, $[\dot{p}_M]$. Bernard et al. (2011) reports the highest values for both parameters, followed by Ren & Schiel (2008) and the "add_my_pet" collection. Both

parameters compete with each other in terms of energy balance. A high $\{\dot{p}_{Xm}\}$ implies a high energy uptake and a high $[\dot{p}_M]$, high somatic maintenance costs. Therefore the covariation of the parameters can compensate each other and provide the same net energy balance. This highlights the potential to apply different sets of parameters but obtain identical outcomes and suggests the need for different pieces of information, i.e. clearance and respiration rates, to disentangle this mathematical artefact derived from parameter covariation.

The sensitivity test (Table 5) showed very similar results to *M. edulis*, that is, a significant impact of ingestion/assimilation and temperature on oyster performance. In both cases, the sensitivity tests are in good agreement with the main controversy in the literature regarding maximum surface area-specific ingestion rate, $\{\dot{p}_{Xm}\}$, which shows an extremely wide range of values for these two species. Due to the direct effect of *AE* on assimilated energy, $\{\dot{p}_{Am}\} = AE\ \{\dot{p}_{Xm}\}$, this parameter, which is usually considered constant and around 0.75, becomes relevant for both species. Regarding the effects of temperature, oysters seem less sensitive than mussels with this current parameterization and under the environmental conditions of Baynes Sound. This suggests that the average temperature regime in Baynes Sound is farther from the upper tolerance threshold in oysters than in mussels (Figure 2).

### 3.3. Clams

#### 3.3.1. Manila (*Venerupis philippinarum)*

Although *V. philippinarum*, *Tapes philippinarum* and *Ruditapes philippinarum* are the same species, the original nomenclature used in each reviewed paper has been maintained in this analysis. In addition, the review of available data has been extended to other similar species, namely, *Ruditapes decussatus* and *Venerupis pullastra*, assuming that their physiology is similar enough for a screening exercise of DEB parameters. Flye-Sainte-Marie (2008) published a DEB model for *R. philippinarum* (Table 6) using the original code on which "add_my_pet" is based. Flye-Sainte-Marie (2008) parameters are significantly different than the current ones reported in the "add_my_pet" portal. A thorough literature review has been done with the aim of re-analyzing the parameter range with focus on the key parameters that may be more sensitive in DEB according to previous simulations in mussels and oysters, that is, maximum surface area-specific ingestion rate, absorption efficiency and temperature. This review was used to define new parameter ranges (Table 6) to be used in the subsequent calibration process. From Coutteau et al. (1994) and Sorokin & Giovanardi (1995) it was estimated that $\{\dot{p}_{Xm}\}$ of *T. philippinarum* could reach 252 and 259 J $d^{-1}$ $cm^{-2}$, respectively. Li et al. (2002) reported a minimum *AE* value of 0.65 (*R. philippinarum*) and Spillman et al. (2008) reported a maximum of 0.8 (*T. philippinarum*). $T_A$ was estimated from physiological rates (clearance, respiration and excretion rates) of *R. philippinarum* at different temperatures (Han et al. 2008). Solidoro et al. (2000) provided a comprehensive dataset of the effects of temperature on respiration rate of *T. philippinarum* that was used to estimate $T_L$, $T_H$, $T_{AL}$ and $T_{AH}$ and expand the existing parameter range. In addition, the range of other less sensitive parameters was also revisited. $[\dot{p}_M]$ is estimated to be within the range 23.4 - 58.1 J

$cm^{-3}$ $d^{-1}$ in the case of *R. decussatus* and *V. pullastra*, according to Albentosa et al. (2007). No data was available regarding $[E_G]$ and consequently the parameter range was expanded following values for other bivalves to 1900-6500 J $cm^{-3}$. According to other bivalves, the range for the minimum DW:WW value was also expanded to 0.1. Finally, after a preliminary run of the calibration process, the minimum $\kappa$ observed in Flye-Sainte-Marie (2008), 0.89, seemed to be too high. Consequently, a minimum $\kappa$ of 0.45, based on the range of values observed for other bivalve species (Table 2, 4), was used instead.

With the new range of parameters (Table 6), a calibration exercise was performed based on the analysis of 100,000 randomized sets of parameters (see above). The goal was to find a set of parameters that could simultaneously explain the growth curves of *R. philippinarum* observed in Flye-Sainte-Marie (2008) and Robert et al. (1993). Flye-Sainte-Marie (2008) data set consists of three independent growth curves with information on shell length and tissue dry weight. Robert et al. (1993) contains four datasets with shell growth but only one of them includes tissue dry weight. The parameters of the best 10 simulations were used to provide the average set (Table 6). The growth trajectories of the parameter set that reported the lowest deviation (see above) is also plotted in Figure 4 and 5 for Flye-Sainte-Marie (2008) and Robert et al. (1993), respectively. The agreement in shell length between observations and simulations is remarkable with the exception of the Gorp87 dataset. An explanation for the mismatch in this dataset is not obvious. Observations suggest a reduced growth rate but available food, expressed as chlorophyll concentration, seems high enough to support bivalve growth. The other forcing function, temperature, does not show any unusual pattern that could explain the growth. Further investigation would be required but it is beyond the goal of this study. Regarding the simulations of tissue dry weight (DW) it is important to clarify that for simplicity the reproductive module of the model has not been activated during these simulations. The thresholds of environmental variables that trigger spawning in bivalve populations are not that clear and consequently spawning in DEB modelling is usually forced on a specific date based on empirical information (e.g. Rosland et al. 2009). The lack of spawning in the model explains the disagreement with observations once that spawning is observed in the field. However, given that DEB allocates energy in different state variables, the reproduction compartment (Figure 1) has been subtracted from the total DW and plotted in Figures 4 and 5. The results suggest that the observed DW is within the range of total DW and DW without gonads, which is logical. Again, further calibration of spawning would improve these simulations but it is beyond the goal of this study.

A sensitivity analysis (Table 7) has been performed to the best set of parameters calculated in the calibration exercise. Once again, $\{\dot{p}_{Xm}\}$ and *AE* became the most relevant parameters, which demonstrates the importance of energy assimilation. The good quality data provided in Solidoro et al. (2000) and Han et al. (2008) that was available to parameterize the effect of temperature reduced the impact of the related parameters on the model. This also suggests that the temperatures of Baynes Sound are not close to any of the tolerance thresholds of Manila clam.

### 3.3.2. Littleneck (*Protothaca staminea)*

There are no DEB models available for the littleneck clam. Accordingly, a thorough literature review has been carried out with the aim of gathering enough datasets to define a potential range of parameters that could be used in a mathematical calibration. Given the similitudes in morphology and growth between Manila and littleneck clams, one possible solution could be to use the Manila set of parameters to calibrate a littleneck model using mathematical algorithms. Nevertheless, data comparing both species is lacking in the literature and consequently this procedure could not be validated. In any case, the available studies with information related to the littleneck clam in the context of DEB modelling have been grouped by topics:

- Growth curves: Information regarding littleneck clam can be obtained from DFO intertidal clam surveys (e.g. Gillespie and Bourne 2000 among others), which provide growth curves of shell length year class although information on weight and environmental conditions is not available.
- Maximum surface area-specific ingestion rate, $\{\dot{p}_{Xm}\}$: Jennings (2012) provides some information on clearance rate. This document is a thesis dissertation, and primary publications of this work are not presently available. The lack of validation of the methods used to measure CR increases the uncertainty in the observed values. In addition, further information would be required to estimate maximum ingestion, and it is not available in the dissertation.

### 3.3.3. Varnish (*Nuttallia obscurata)*

In the same way as for littleneck clams, there are no DEB models available for varnish clams. A similar literature review has identified the following datasets that could potentially be used for calibration:

- Growth curves: Gillespie et al. (1999, 2001) and Gordon et al. 2015 (and related DFO documents/reports) provide some information on shell growth by year class but information on weight and environmental conditions is absent. Lum (2006) also provides some information on weekly growth rates. Nevertheless, all the above datasets are incomplete for use in the context of DEB modelling, which requires growth but also a description of the environmental conditions at least in terms of food density and temperature.
- Temperature: Dudas (1997) provides some information on the effect of temperature (3 temperatures) on larval growth. This data set seems relevant to the estimation of the Arrhenius temperature. However, it should be completed by data on different types of rates. It also provides biometric data (growth curves, weight vs. length) as well as information on reproductive activity which is usually rather rare.
- Shape coefficient, $\delta_M$: All previous papers with the exception of Lum (2006) provide allometric relationships between length and dry weight but none of them with wet weight. Therefore additional assumptions would be required to estimate $\delta_M$.

- Maximum surface area-specific ingestion rate, $\{\dot{p}_{Xm}\}$: Only two research documents have investigated clearance rates (CR) of varnish clams (Jennings 2012, Talkington 2015). Talkington (2015) is also a thesis dissertation and presents the same problems as Jennings (2012) (see above).

### 3.3.4. Butter (*Saxidomus gigantea*)

Similarly, there are no DEB models for butter clam. Potential datasets to define parameter ranges are:

- Growth curves: Few datasets with short-term growth rates or long term but without associated environmental data are available (e.g. Walne 1973, Contreras & Dethier 2011). It is important to highlight that Bigg (2002) and Goong & Chew (2001) provide von Bertalanffy growth models, which could be useful for a general calibration given that DEB provides a mechanistic explanation of the von Bertalanffy model in the case of isomorphs that experience constant food availability.
- Maximum surface area-specific ingestion rate, $\{\dot{p}_{Xm}\}$: in addition to Jennings (2012) who also provides data for butter clams, Bernard & Noakes (1990) report valuable information on clearance (also respiration) rates. Nevertheless ingestion cannot be calculated and according to the methods it seems that only one individual was used in this experiment.

## 4.0. CONCLUSIONS

The available sets of DEB parameters for the mussel *M. edulis* and the oyster *C. gigas* provide a solid foundation to apply optimization tools with the aim of calibrating a DEB model for BC waters populations. In the case of the clam *V. philippinarum* the available set of parameters and the extensive literature on Manila clams also yield enough information to restrict future data collection to calibration/validation purposes and not to specific parameters. Nevertheless, in order to minimize the uncertainty of a calibration purely based on mathematical algorithms, the validation datasets must include physiological rates, and at least some seasonal insight on clearance, respiration and excretion rates, in addition to growth curves and associated environmental conditions. On the contrary, in the case of the clams *P. staminea*, *N. obscurata* and *S. gigantea*, additional datasets are required to set bounds to DEB parameters. Specifically for *P. staminea* a comparative study with *V. philippinarum* could be performed using the same range of parameters for calibration. Ideally, the following datasets would be required:

- Growth curves: length and weight over time with simultaneous environmental monitoring (seston, chlorophyll and temperature) for calibration and validation. More than one dataset is required, which could be different locations or the same location during different years.

- Seasonal allometries: Length-wet weight, length-dry weight, length-ash free dry weight, length-width, length-area, length-volume relationships at different times of the year to (1) estimate the shape coefficient, $\delta_M$, and maximum storage density, $[E_m]$, by comparing lowest vs highest condition; and (2) gain some insight on gonadosomatic index and reproductive cycle, which would help to improve the calibration of $\kappa$.
- Ingestion experiment: clearance, ingestion and absorption rates during the spring bloom (or period of maximal growth) to estimate maximum ingestion and assimilation rates, $\{\dot{p}_{Xm}\}$ and $\{\dot{p}_{Am}\}$, respectively.
- Starvation experiment: starvation experiment with regular monitoring of respiration rates to (1) estimate volume-specific maintenance costs, $[\dot{p}_M]$, and (2) measure energy content of the structural body mass of an individual after starvation, just before mortality, to estimate volume-specific costs for growth, $[E_G]$.
- Temperature experiment: respiration rates of starved individuals acclimated to a broad range of temperatures to estimate Arrhenius temperature and associated parameters ($T_A$, $T_L$, $T_H$, $T_{AL}$ and $T_{AH}$). Although respiration rate is recommended for this purpose, given that it provides information regarding basal metabolism, any other physiological rate could be used instead for the estimation of the Arrhenius temperature.

These experiments would provide a comprehensive dataset with which to set up a DEB model. Data gaps could be overcome by the use of mathematical algorithms for calibration purposes. However, it is important to highlight the value of growth curves as the central datasets for calibration and validation. Therefore, a good characterization of growth in relation to environmental conditions must be prioritized. The information of these discrete datasets and the simultaneous inclusion of all of them in the same calibration procedure (e.g. add_my_pet) constitutes an ideal path to construct DEB models.

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**Table 1:** Equations of the Dynamic Energy Budget (DEB) model.

| Equation | Terms and parameters | |
|---|---|---|
| $\frac{dE}{dt} = \dot{p}_A - \dot{p}_C$ | $E$ | Reserve (J) |
| | $\dot{p}_A$ | assimilation rate (J $d^{-1}$) |
| | $\dot{p}_C$ | mobilization rate of reserve energy (J $d^{-1}$) |
| | $\{\dot{p}_{Am}\}$ | maximum surface-area-specific assimilation rate (J $cm^{-2}$ $d^{-1}$) |
| $\dot{p}_A = \{\dot{p}_{Am}\} T_D f V^{2/3}$ | $f$ | Functional response |
| | $V$ | structural volume ($cm^3$) |
| | $T_D$ | Arrhenius temperature function |
| $f = \frac{X}{X + X_K}$ | $X$ | Chlorophyll concentration (µg $l^{-1}$) |
| | $X_K$ | Half-saturation constant (µg $l^{-1}$) |
| | $\kappa$ | fraction of utilized energy to somatic maintenance and growth |
| $\dot{p}_C = \frac{[E]}{[E_G]+\kappa[E]} \left( \frac{[E_G]\{\dot{p}_{Am}\} T_D V^{2/3}}{[E_m]} + \dot{p}_M \right)$ | $[E_G]$ | volume-specific costs for structure (J $cm^{-3}$) |
| | $[E_m]$ | maximum energy density (J $cm^{-3}$) |
| $\dot{p}_M = [\dot{p}_M] T_D V$ | $\dot{p}_M$ | maintenance rate (J $d^{-1}$) |
| | $[\dot{p}_M]$ | volume-specific maintenance costs (J $cm^{-3}$ $d^{-1}$) |
| $\frac{dV}{dt} = (\kappa \dot{p}_C - \dot{p}_M) / [E_G]$ | | |
| $\frac{dE_R}{dt} = (1-\kappa)\dot{p}_C - \left( \frac{1-\kappa}{\kappa} \right) \cdot V \cdot [\dot{p}_M]$ | $E_R$ | energy allocated to reproduction buffer (J) |
| $\frac{dE_R}{dt} = \kappa \dot{p}_C - \dot{p}_M \mid \kappa \dot{p}_C - \dot{p}_M < 0$ | | reproduction buffer dynamics when energy storage is too low |
| $L = \frac{V^{1/3}}{\delta_M}$ | $L$ | filter-feeder length (cm) |
| | $\delta_M$ | dimensionless shape coefficient |

**Table 2:** *Mytilus edulis* DEB parameters.

| | Data source | | | | |
|---|---|---|---|---|---|
| Parameter | van der Veer et al. 2006 | Rosland et al. 2009 | Saraiva et al. 2011 | Maar et al. 2015 | add_my_pet |
| $\delta_M$ | 0.287 | 0.231 | 0.297 | 0.248-0.305 | 0.294 |
| $\{\dot{p}_{Xm}\}$ | 197 | 273 | 107 | 488 | 150 |
| $[\dot{p}_M]$ | 24 | 27.8 | 11.6 | 11.6 | 13.7 |
| $[E_G]$ | 1900 | 1900 | 5993 | 5993 | 4783 |
| $[E_m]$ | 2203 | 2170 | 1438 | 1438 | 1105 |
| $\kappa$ | 0.7 | 0.45 | 0.67 | 0.67 | 0.81 |
| $X_K$ | calibration | calibration | N/A | 1 | 0 |
| $T_A$ | 5800 | 5800 | 7022 | 5800 | 7022 |
| $T_L$ | 275 | 275 | N/A | 275 | 275 |
| $T_H$ | 296 | 296 | N/A | 296 | 296 |
| $T_{AL}$ | 45430 | 45430 | N/A | 45430 | 45430 |
| $T_{AH}$ | 31376 | 31376 | N/A | 31376 | 31376 |
| $AE$ | 0.75 | 0.75 | 0.75[1] | 0.8 | 0.53 |
| DW:WW | 0.2 | 0.2 | 0.2 | 0.1-0.26 | 0.12 |

[1]assumed

**Table 3:** Maximum change in final shell length (SL), dry weight (DW), dry weight minus gonads (DWmG), clearance rate (CR), respiration rate (RR) and excretion rate (ER) of *Mytilus edulis* after a ±10% in parameter.

| | Maximum change (%) after a ±10% in parameter | | | | | |
|---|---|---|---|---|---|---|
| Parameter | SL | DW | DWmG | CR | RR | ER |
| $\delta_M$ | 9.4 | 4.8 | 5.1 | 3.3 | 3.5 | 5.0 |
| $\{\dot{p}_{Xm}\}$ | 7.5 | 24.0 | 24.4 | 27.2 | 26.9 | 24.3 |
| $[\dot{p}_M]$ | 2.0 | 4.5 | 6.1 | 4.0 | 3.4 | 4.6 |
| $[E_G]$ | 4.9 | 12.2 | 15.5 | 10.1 | 9.4 | 15.4 |
| $[E_m]$ | 1.2 | 1.7 | 0.4 | 2.3 | 3.3 | 3.5 |
| $\kappa$ | 6.6 | 8.5 | 20.6 | 13.3 | 11.9 | 20.4 |
| $X_K$ | 1.0 | 3.3 | 3.6 | 4.0 | 3.7 | 3.0 |
| $T_A$ | 3.6 | 12.0 | 11.1 | 18.6 | 18.8 | 22.8 |
| $T_L$ | 0.1 | 0.3 | 0.3 | 0.7 | 0.7 | 0.8 |
| $T_H$ | 15.1 | 57.4 | 52.2 | 75.1 | 76.7 | 101.1 |
| $T_{AL}$ | 0.3 | 1.0 | 0.9 | 2.1 | 2.1 | 2.4 |
| $T_{AH}$ | 1.0 | 3.3 | 3.1 | 4.8 | 4.9 | 5.9 |
| $AE$ | 7.5 | 24.0 | 24.4 | 15.7 | 26.9 | 24.3 |
| DW:WW | 0.2 | 3.6 | 6.6 | 0.3 | 0.3 | 0.5 |

**Table 4:** *Crassostrea gigas* DEB parameters.

| | Data source | | |
|---|---|---|---|
| Parameter | Bernard et al. 2011 | Ren & Schiel 2008 | add_my_pet |
| $\delta_M$ | 0.175 | 0.21 | 0.121 |
| $\{\dot{p}_{Xm}\}$ | 1027 | 894 | 187.3 |
| $[\dot{p}_M]$ | 44 | 22.5 | 12.7 |
| $[E_G]$ | 3900-7500[1] | 2900 | 2674 |
| $[E_m]$ | 4200 | 5900 | 7602 |
| $\kappa$ | 0.45 | 0.65 | 0.29 |
| $X_K$ | calibration | 1.9 | 0 |
| $T_A$ | 5800 | 5900 | 8000 |
| $T_L$ | 281 | 283 | 273 |
| $T_H$ | 298 | 303 | 400[4] |
| $T_{AL}$ | 75000 | 13000 | 50000 |
| $T_{AH}$ | 30000 | 80000 | 190000 |
| $AE$ | 0.75 | 0.75[3] | 0.3259 |
| DW:WW | 0.15-0.31[2] | 0.2 | N/A |

[1]3900-7500 cost for structure and gonads, respectively
[2]0.15-0.31 for structure and gonads, respectively
[3]assumed
[4]this extreme value is intentionally unrealistic to reflect the uncertainty in the parameter

**Table 5:** Maximum change in final shell length (SL), dry weight (DW), dry weight minus gonads (DWmG), clearance rate (CR), respiration rate (RR) and excretion rate (ER) of *Crassostrea gigas* after a ±10% in parameter.

| | Maximum change (%) after a ±10% in parameter | | | | | |
|---|---|---|---|---|---|---|
| Parameter | SL | DW | DWmG | CR | RR | ER |
| $\delta_M$ | 9.3 | 4.6 | 5.3 | 3.5 | 3.7 | 5.1 |
| $\{\dot{p}_{Xm}\}$ | 6.3 | 19.3 | 20.0 | 24.3 | 23.7 | 19.5 |
| $[\dot{p}_M]$ | 1.6 | 4.2 | 4.8 | 3.2 | 2.2 | 5.8 |
| $[E_G]$ | 3.8 | 10.3 | 11.9 | 7.8 | 6.5 | 11.5 |
| $[E_m]$ | 1.7 | 1.9 | 1.2 | 3.4 | 5.1 | 5.0 |
| $\kappa$ | 5.3 | 7.1 | 15.8 | 10.3 | 8.4 | 13.9 |
| $X_K$ | 0.7 | 2.6 | 2.8 | 3.4 | 2.8 | 2.1 |
| $T_A$ | 2.4 | 7.3 | 7.3 | 13.6 | 13.8 | 16.1 |
| $T_L$ | 0.5 | 1.5 | 1.4 | 3.6 | 3.6 | 4.0 |
| $T_H$ | 3.7 | 11.4 | 11.4 | 18.4 | 18.7 | 22.4 |
| $T_{AL}$ | 0.7 | 2.1 | 2.1 | 3.9 | 3.9 | 4.5 |
| $T_{AH}$ | 0.7 | 2.1 | 2.1 | 3.7 | 3.7 | 4.3 |
| $AE$ | 6.3 | 19.3 | 20.0 | 13.0 | 23.7 | 19.5 |
| DW:WW | 0.2 | 4.3 | 5.8 | 0.4 | 0.4 | 0.5 |

**Table 6:** *Venerupis philippinarum* DEB parameters.

| | Data source | | | | |
|---|---|---|---|---|---|
| | | | Tested parameters | | |
| Parameter | Flye-Sainte-Marie 2008 | add_my_pet | Minimum | Maximum | Best solutions |
| $\delta_M$ | 0.29 | 0.352 | 0.29 | 0.36 | 0.33±0.01 |
| $\{\dot{p}_{Xm}\}$ | 96.3 | 3.7 | 3.7 | 259 | 199±17 |
| $[\dot{p}_M]$ | 24.66 | 28.24 | 23.4 | 58.1 | 38.0±9.4 |
| $[E_G]$ | 2710 | 3050 | 1900 | 6500 | 5200±802 |
| $[E_m]$ | 2200 | 227.5 | 227 | 2200 | 787±456 |
| $\kappa$ | 0.89 | 0.987 | 0.45 | 0.99 | 0.55±0.09 |
| $X_K$ | calibration | 0 | 0 | 3 | 0.49±0.37 |
| $T_A$ | 6071 | 6071 | 6071 | 8665 | 7571±789 |
| $T_L$ | 275 | 273 | 273 | 278 | 275.3±1.3 |
| $T_H$ | 300 | 400[1] | 297 | 299 | 298.1±0.6 |
| $T_{AL}$ | 299859 | 50000 | 100000 | 299859 | 2.1E5±5.5E4 |
| $T_{AH}$ | 30424 | 190000 | 30424 | 50000 | 3.7E4±4.7E3 |
| $AE$ | 0.89 | 0.7 | 0.65 | 0.80 | 0.72±0.03 |
| DW:WW | 0.216 | 0.12 | 0.1 | 0.216 | 0.12±0.02 |

[1] this extreme value is intentionally unrealistic to reflect the uncertainty in the parameter

**Table 7:** Maximum change in final shell length (SL), dry weight (DW), dry weight minus gonads (DWmG), clearance rate (CR), respiration rate (RR) and excretion rate (ER) of *Venerupis philippinarum* after a ±10% in parameter

| | Maximum change (%) after a ±10% in parameter | | | | | |
|---|---|---|---|---|---|---|
| Parameter | SL | DW | DWmG | CR | RR | ER |
| $\delta_V$ | 8.4 | 7.9 | 8.3 | 5.4 | 5.5 | 8.3 |
| $\{\dot{p}_{Xm}\}$ | 7.3 | 22.6 | 23.6 | 26.7 | 26.5 | 23.6 |
| $[\dot{p}_M]$ | 5.0 | 8.5 | 15.8 | 10.3 | 10.0 | 4.4 |
| $[E_G]$ | 2.4 | 5.3 | 7.5 | 4.9 | 4.9 | 7.5 |
| $[E_m]$ | 0.2 | 0.2 | 1.6 | 0.4 | 0.6 | 0.6 |
| $\kappa$ | 7.1 | 2.1 | 22.9 | 14.7 | 14.4 | 22.9 |
| $X_K$ | 1.0 | 2.9 | 3.5 | 4.0 | 4.0 | 3.0 |
| $T_A$ | 0.8 | 4.3 | 2.3 | 9.9 | 10.0 | 10.7 |
| $T_L$ | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| $T_H$ | 0.4 | 2.5 | 1.2 | 13.1 | 13.2 | 13.6 |
| $T_{AL}$ | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| $T_{AH}$ | 0.1 | 0.8 | 0.4 | 1.8 | 1.8 | 1.9 |
| $AE$ | 7.3 | 22.6 | 23.6 | 15.1 | 26.5 | 23.6 |
| DW:WW | 0.1 | 1.4 | 7.8 | 0.1 | 0.1 | 0.2 |

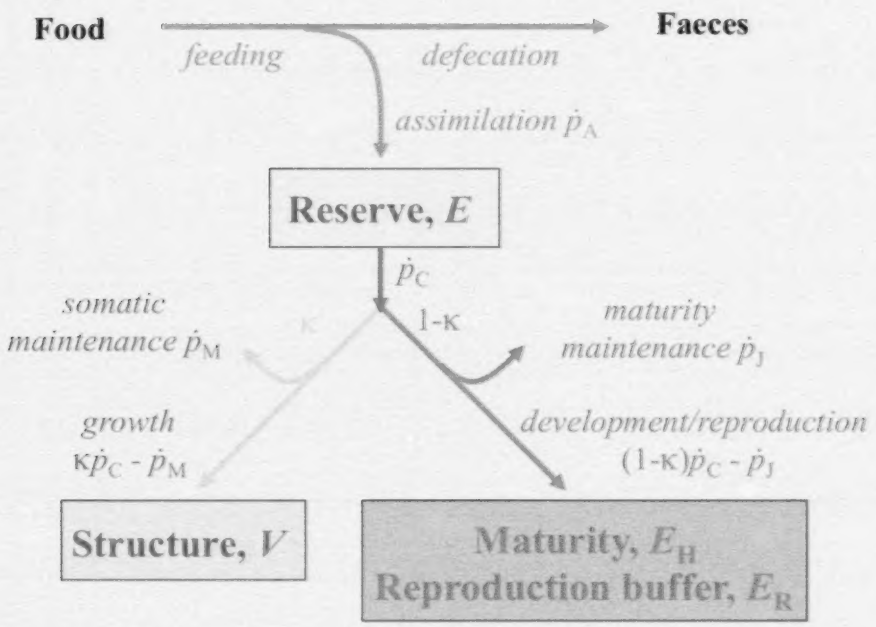


**Figure 1:** Dynamic Energy Budget (DEB) model scheme for juvenile (development/maturity) and adult (reproduction/reproduction buffer) life stages. See Table 1 for differential equations.

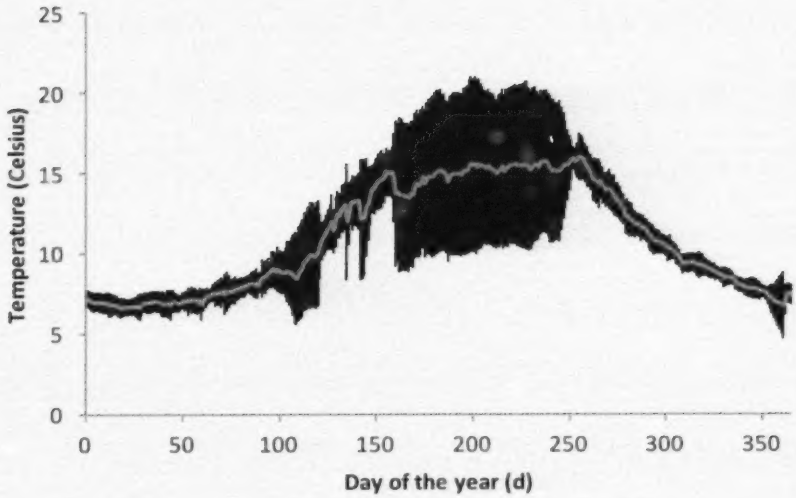


**Figure 2:** Temperature (°C) pattern in Baynes Sound (2002-2015 average). Blue line represents the mean and the black area maximum and minimum.

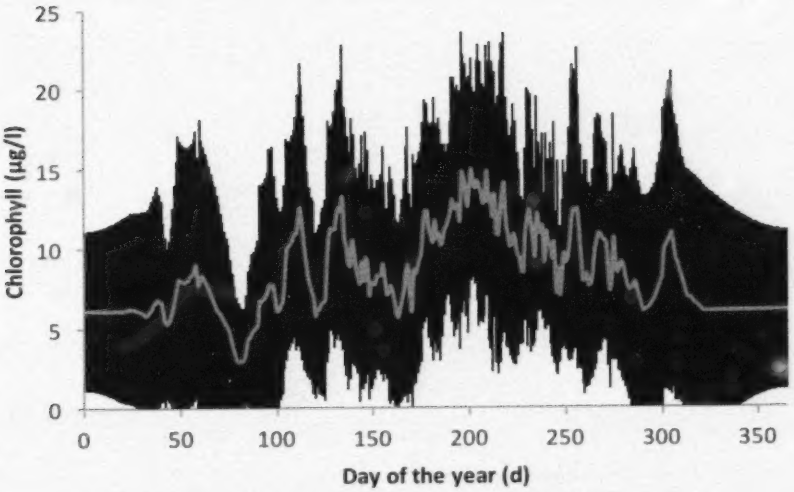


**Figure 3:** Chlorophyll pattern (µg chla $l^{-1}$) in Baynes Sound (2002-2015 average). Blue line represents the mean and the black area maximum and minimum.

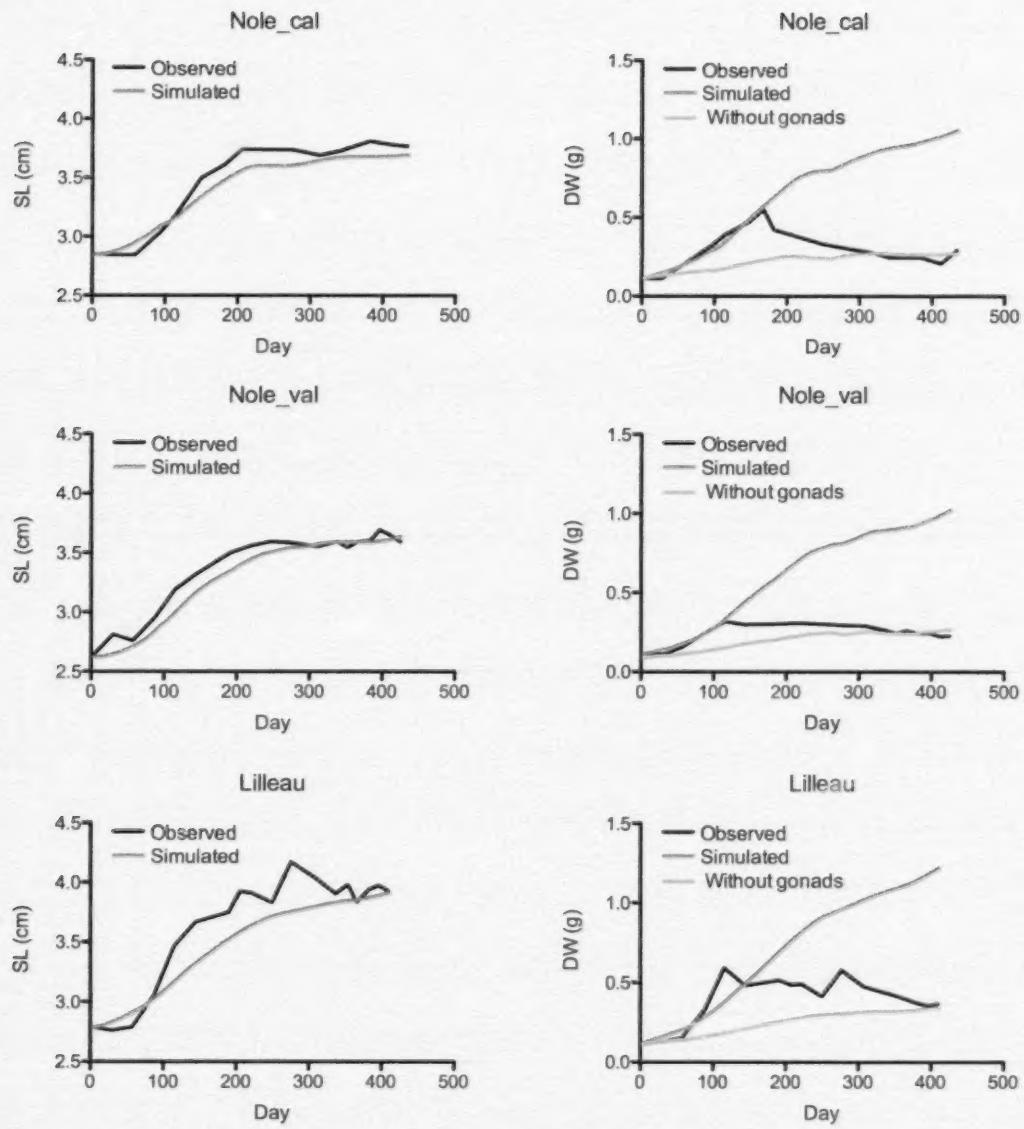


**Figure 4:** Observed (black continuous line) and DEB-simulated (red and orange) growth trajectories (shell length, SL, and tissue dry weight, DW) for Flye-Sainte-Marie (2008) datasets.

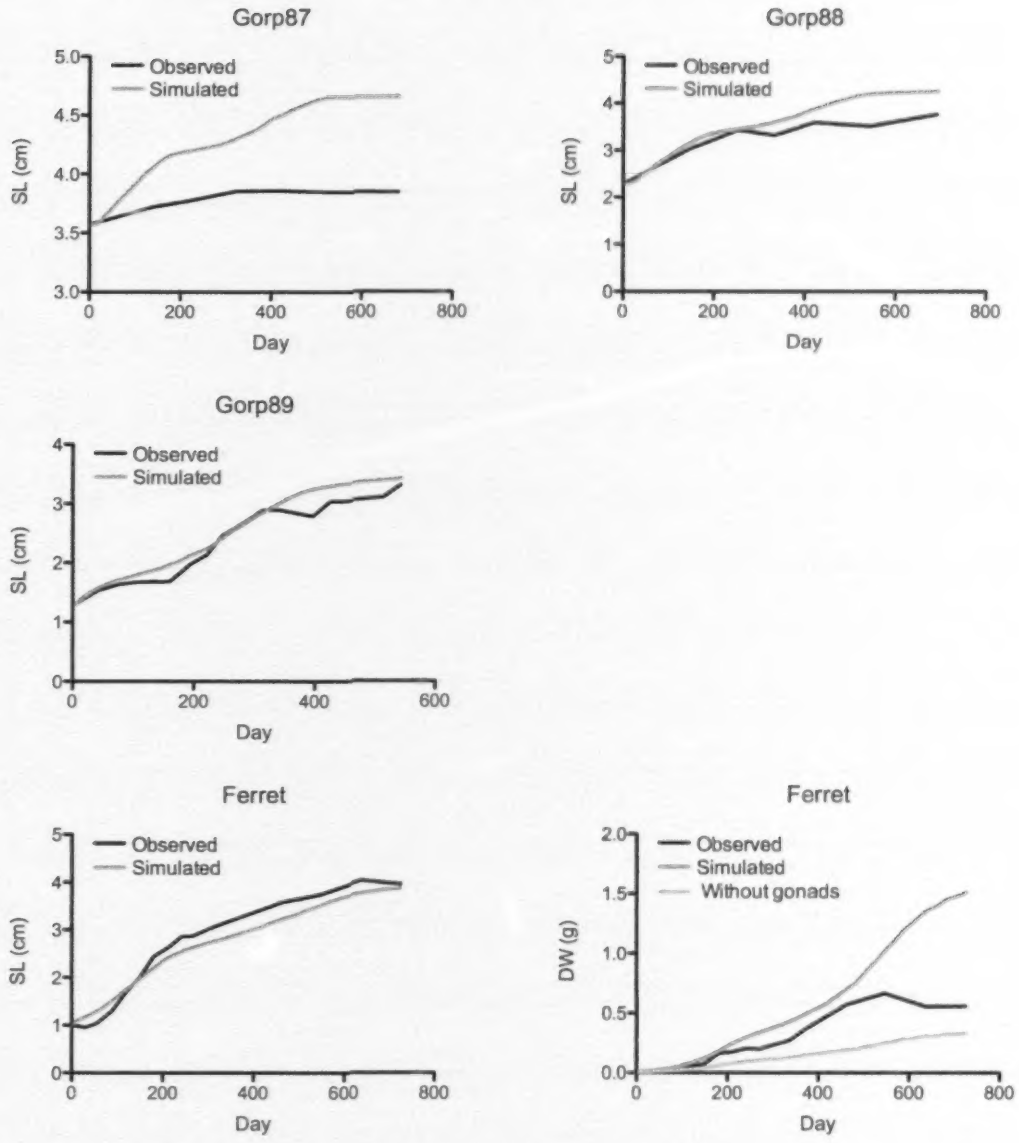


**Figure 5:** Observed (black continuous line) and DEB-simulated (red and orange) growth trajectories (shell length, SL, and tissue dry weight, DW) for Robert et al. (1993) datasets.